Will nutrient-efficient genotypes mine the soil? Effects of genetic differences in root architecture in common bean (*Phaseolus vulgaris* L.) on soil phosphorus depletion in a low-input agro-ecosystem in Central America

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ABSTRACT

Crop genotypes with root traits permitting increased nutrient acquisition would increase yields in low fertility soils but have uncertain effects on soil fertility in the long term because of competing effects on nutrient removal vs. the soil conserving effects of greater crop biomass. This study evaluated the relative importance of phosphorus loss in crop extraction vs. phosphorus loss in soil erosion as influenced by genetic differences in root shallowness and therefore phosphorus uptake in common bean (*Phaseolus vulgaris* L.). Six recombinant inbred lines of varying root architecture and two commercial genotypes of bean were grown in unfertilized, steeply sloped (32%), low phosphorus (5.8 mg kg^{-1}, Fe-strip) Udults in Costa Rica. Fertilized (60 kg total phosphorus ha^{-1}) plots of commercial genotypes were also included in the study. Runoff was monitored throughout the bean growing season in 2005 and 2006, and in 2006, monitoring continued through the maize growing season. Phosphorus removed in plant biomass at harvest through the 2006 bean–maize crop cycle averaged 7.3 kg ha^{-1} year^{-1}, greatly exceeding phosphorus loss due to erosion (0.15–0.53 kg ha^{-1} year^{-1}) in unfertilized plots. In fertilized bean plots, total biomass phosphorus averaged 6.32 kg ha^{-1} year^{-1} and total eroded phosphorus averaged 0.038 kg ha^{-1} year^{-1}, indicating rapid sorption of fertilizer phosphorus. Shoot growth of several recombinant inbred lines under low phosphorus was comparable to that of fertilized commercial genotypes, illustrating the effectiveness of selection for root traits for improving plant growth in low-phosphorus soils. Genotypic differences in root architecture of recombinant inbred lines led to 20–50% variation in groundcover by shoots, which was associated with 50–80% reduction in sediment loss. This study demonstrates that root architecture traits can affect nutrient cycling at the agro-ecosystem level, and that integrated nutrient management strategies are necessary to avoid soil nutrient depletion.

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1. Introduction

Low-phosphorus availability is a primary constraint to crop production in many developing countries (Lynch, 2007). Crop breeding for traits that enhance phosphorus uptake is a promising strategy for improving yields in low-phosphorus soils. While such crops would directly benefit low-input farmers in the short term, their long-term effects on soil fertility are uncertain. Increased phosphorus extraction form the soil may accelerate 'soil mining' and fertility depletion, but increased plant biomass may reduce phosphorus loss by erosion, especially in sloping soils (Lynch, 1998). In low-input systems where phosphorus removal in harvested biomass could be comparable to phosphorus removal by erosion, there is insufficient information to determine how phosphorus-extractive genotypes may affect soil fertility in the long term.

Root architectural traits are key adaptations to phosphorus stress in low-input agro-ecosystems (Lynch and Brown, 2008). Root traits that enhance topsoil foraging are advantageous in low-phosphorus soil since phosphorus bioavailability is typically greatest in surface horizons (Lynch and Brown, 2001). Genotypes with shallow root architecture have greater growth and yield in low-phosphorus soil than related genotypes with deep architectures (Rubio et al., 2003; Miller et al., 2003; Ho et al., 2005; Zhu et al., 2005). Root traits that increase phosphorus acquisition

would directly affect phosphorus removal in harvested seed but are also likely to affect shoot biomass and thereby phosphorus lost to soil erosion. The effect of shoot biomass on soil erosion is important in low-input and degraded agro-ecosystems since shoot growth is one of the most important crop attributes affecting soil erosion by rainfall (Meyer and Mannering, 1971).

Reports of erosional phosphorus loss range widely, including 2.5 kg ha^{-1} year^{-1} estimated for Sub-Saharan Africa (Stoorvogel et al., 1993), up to 5.4 kg ha^{-1} year^{-1} estimated with the RUSLE model in Uganda (Wortmann and Kaizzi, 1998), and up to 13.1 kg ha^{-1} year^{-1} in bare Nigerian alfisols with a 15% slope (Lal, 1976). Values for phosphorus removal in crop harvest also range widely depending on location, soil type, and crop species. In common bean, reports of grain phosphorus contents include 4.5–7.0 kg ha^{-1} in a Typic Haplustult with 3 mg kg^{-1} phosphorus (Araújo and Teixeira, 2003). Most estimates of erosion/soil nutrient depletion are derived from models (i.e., Stoorvogel and Smaling, 1990; Hailesslassie et al., 2005). This is problematic for estimating erosion in the tropics since existing models were primarily developed for temperate ecosystems that may not encompass the precipitation patterns and soil properties of tropical ecosystems. Additional empirical measurements of erosion and soil nutrient budgets are needed, particularly in highly heterogeneous environments such as Central America, to estimate nutrient depletion in tropical agro-ecosystems and to validate models based on temperate data sets.

This study examines differences in phosphorus cycling among common bean genotypes varying in phosphorus efficiency in a low-input maize–bean agro-ecosystem in Veracruz, Costa Rica from 2005 to 2006. We hypothesized that genotypes with shallow root growth would have greater phosphorus uptake, greater shoot growth, and therefore less soil erosion than deep-rooted genotypes. Based on previous nutrient balance calculations (i.e., Stoorvogel and Smaling, 1990), we also hypothesized that in low-input common bean agro-ecosystems with steep slopes, more phosphorus would be lost to erosion than through biomass removal at harvest.

2. Materials and methods

2.1. Experimental setup

Two sites were chosen in the south-central highlands of Costa Rica in the town of Veracruz (9°05′30″N, 83°32′39″W) based on low-phosphorus availability, steep slopes, and history of low-input agricultural management. Average annual rainfall is 2400 mm (Hernández et al., 1999). Site 1 was cleared of forest around 1960, and since then has been under a maize bean rotation. Site 2 was cleared around 1957, then maintained as a pasture until a maize bean rotation was initiated 5 years before the start of this study. Soils at both sites were classified as Udults.

Forty 4 m × 7 m runoff plots were established, with 3 m × 5 m surrounded by sheet metal (20 cm wide) to form a hydrologically isolated runoff collection area, and fitted with 60-L runoff collection buckets at the downslope end (Fig. 1). Sixteen plots were installed at Site 1 and 24 plots at Site 2, for a total of 40 experimental runoff plots. Both sites were uniform in slope, and the average slope of all plots was 32.4 ± 0.69% as determined with an optical reading clinometer (Suunto PM-5). Baseline extractable phosphorus levels averaged 7.9 ± 1.3 mg kg^{-1} at Site 1 and 4.4 ± 0.4 mg kg^{-1} at Site 2, which are slightly lower than the regional average of about 10 mg kg^{-1}, but well below recommended Mehlich-III extractable phosphorus levels of 45–50 mg kg^{-1} for optimum productivity (Sims, 2000). Percent organic matter (g OM 100 g^{-1} soil) averaged 7.15 ± 0.17 at Site 1 and 10.0 ± 0.25 at Site 2. The pre-

season soil analysis conducted in 2005 showed low pH at both sites (Table 1).

This study was conducted during the bean season (primera: May through August) in 2005 and 2006, as well as during the maize season (postrera: September through December) in 2006. Six recombinant inbred lines of common bean from the L-88 population (supplied by Dr. James Kelly, Michigan State University) and two elite commercial bean genotypes, Bribri and DOR364, were grown with four replicate plots per genotype for the low-phosphorus treatment (no fertilizer applied). These L-88 genotypes were chosen based on observed differences in phosphorus efficiency and root architecture in previous studies (Ho et al., 2005; Henry et al., 2009). The L-88 population is derived from a cross between genotypes B98311, which was bred for drought resistance, and TLP 19, bred for adaptation to low-phosphorus availability (Frahm et al., 2004). The CIAT derived elite genotype DOR364 is known to be phosphorus-inefficient due to its deep root architecture (Bonser et al., 1996), whereas Bribri is currently one of the most productive genotypes used by local small-scale growers (Hernández and Elizondo, 2006). An additional four plots each of Bribri and DOR364 were planted and supplemented with fertilizer (high-P treatment). For the maize runoff study in 2006, seven plots at Site 1 were planted with 'Diamantes 8843' (INTA, Costa Rica), and 13 plots were planted at Site 2 with the commercial genotype 'Sangre de Gallo,' all under low phosphorus.

A randomized block design was used for the L-88 RILs, with plots for one block arranged in the same row along the slope. One block was located at Site 1 and three blocks were located at Site 2. The experimental design was completely randomized for elite bean genotypes (low and high-P treatments; Fig. 1) and the maize study. A total of four replicate plots for each bean treatment and 20 replicate plots of maize were planted.

Crops were managed according to standard methods used by growers in the region, which is completely un-mechanized, in order to acquire results that are relevant to understanding phosphorus cycles in these low-input agro-ecosystems. Seeds were planted by hand with an espeque (wooden rod with a small blade at the end) in a grid pattern into untilled soil, with 2–3 seeds placed in a small hole and 40-cm spacing between holes. Organic matter from previous crops was present on the soil surface, some of which was removed from plots when present in excess amounts compared to other plots. For the high-P commercial genotype plots, 10-30-10 fertilizer was applied to the soil surface at a rate of 200 kg ha^{-1} (60 kg P ha^{-1}). In 2005, fertilizer application was immediately followed by a heavy rain and was subsequently re-applied to ensure a treatment effect. Pests and pathogens were managed using insecticides terbufos (1 kg ha^{-1}) and deltametrina (0.012 kg ha^{-1}), and the fungicides azoxistrobina (0.05 kg ha^{-1}), benomyl (0.5 kg ha^{-1}), and mancozeb (0.4 kg ha^{-1}). Herbicides glyphosate (0.81 kg ha^{-1}) and paraquat (0.17 kg ha^{-1}) were applied before planting. In the 2005 bean and 2006 maize seasons, weed management followed regional practices where weeds are controlled until flowering by manual cultivation. In 2006, weeds were controlled throughout the bean season. Rainfall amount and intensity were recorded in 2006 with a tipping bucket pluviometer (Onset Inc., Bourne MA, USA; model RG2), and manual rain gauge readings were recorded daily in 2005 and 2006.

2.2. Plant measurements

Plant tissue was sampled from three border plants mid-season and five within-plot plants at harvest (70 and 77 days after planting (DAP) in 2005, 50 and 81 DAP in 2006) for common bean, and three plants at harvest (125 DAP) for maize in 2006. Plant samples were separated by tissue type (i.e., leaf, stem, and pod),
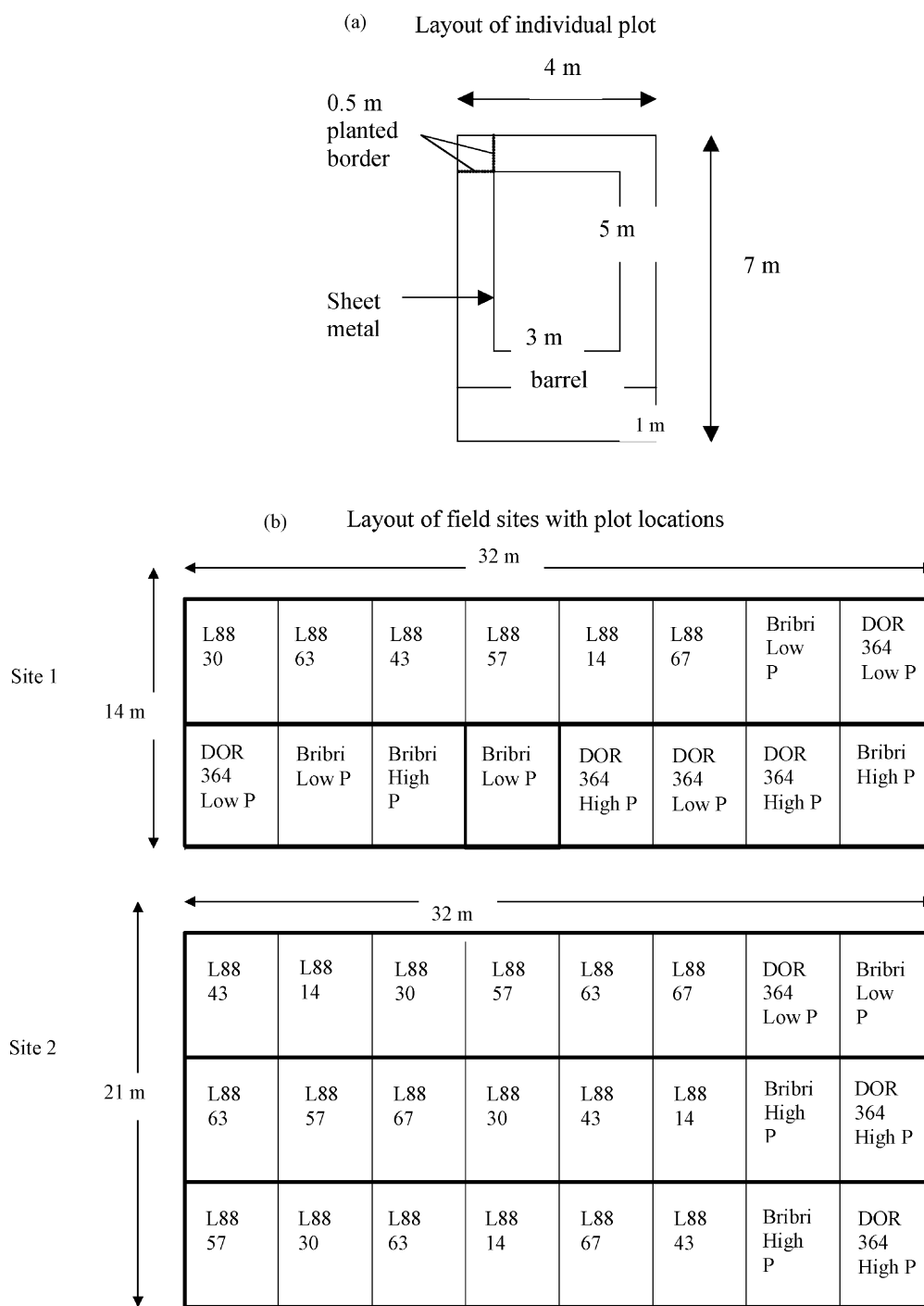
(a)   Layout of individual plot

(b)   Layout of field sites with plot locations

Fig. 1. (a and b) Forty runoff plots were installed at two sites in Veracruz, Costa Rica in 2005 and 2006. Plots of L-88 RILs were arranged in a randomized block design, and plots of commercial genotypes (high and low P) were arranged in a completely randomized design.

Table 1
Properties of field soils at time of planting in 2005. Nutrient availability and CEC was determined by Mehlich-3 extraction, pH was determined in water (1:1). Values shown are average of blocks ± standard error.

Soil property	Site 1	Site 2
pH	5.5 ± 0.3	4.9 ± 0.1
P, mg kg^{-1}	10 ± 4.0	8.3 ± 1.2
K, mg kg^{-1}	528 ± 176	313 ± 22.6
Mg, mg kg^{-1}	565 ± 43	648 ± 33
Ca, mg kg^{-1}	2826 ± 80	2238 ± 104
CEC, mequiv. kg^{-1}	288 ± 15	308 ± 5.5

dried at 60 °C, and weighed. Subsamples were shipped to Penn State University where they were ashed for 15 h at 500 °C, suspended in 100 mM HCl, and used for colorimetric phosphorus analysis according to Murphy and Riley (1962) using a UV-VIS Spectrophotometer (Perkin Elmer, Waltham MA, USA). Samples acquired at harvest were representative of the amount of plant tissue removed through typical local harvesting practices, which includes removal of crown roots, in order to understand the complete phosphorus cycle. The average mass of each tissue type was used to scale up for calculation of the whole-plot P budget, based on the number of plants per plot (determined at harvest). Total yield from each entire plot was also measured at harvest.

Phosphorus harvest index (PHI) was calculated from the phosphorus in the harvested grain (kg) divided by the phosphorus content in the whole shoot (kg) at harvest.

Groundcover was measured on two dates in 2005 and seven dates in 2006 for common bean. A digital overhead image acquired from a 0.6 m^2 area within each plot was subject to color analysis in WinRhizo Pro (version 2002c, Régent Instruments, Quebec) in order to distinguish plant tissue, organic matter, and soil in each image. Images from 2005 were also manually analyzed using Photoshop (Adobe Inc.) to distinguish bean plant and weed cover according to Klassen et al. (2003).

Soil cores were collected to determine root length density in the border of plots of L-88 RILs (2005 and 2006) and commercial bean genotypes (2006) using a 4-cm diameter soil corer (Giddings Machine Co., Windsor CO, USA) mid-way between plants. Soil cores were collected from 3 to 4 replicates of L-88 RILs, and 2–3 replicates of commercial bean genotypes, from one core per plot around the time of flowering. Soil cores were kept shaded until roots were washed from the soil at depth increments of 0–15, 15–30 and 30–45 cm. Root samples were stored in 25% ethanol until stained with neutral red (0.162 g L^{-1}), scanned and analyzed using WinRhizo (Régent Instruments, Quebec, Canada) to determine total root length per core section (cm root cm^{-3} soil). Roots were then dried and weighed to determine specific root length (m g^{-1}).

2.3. Soil and runoff measurements

Pre-season soil samples were acquired in 2005 from a depth of 0–20 cm with a Dutch auger at each site as a composite of a linear transect across each block, with one sample per plot (eight composited samples per block). All samples were air-dried at 40 °C and sieved (2 mm) before analysis. Samples were extracted with Mehlich-3 solution (0.2 M CH_3COOH + 0.25 M NH_4-NO_3 + 0.015 M NH_4F + 0.013 M HNO_3 + 0.001 M EDTA) by shaking 1.0 g of soil with 10 mL of solution for 5 min (Mehlich, 1984). Extract phosphorus, potassium (K), calcium (Ca), and magnesium (Mg) were determined by inductively coupled plasma-optical emission spectroscopy. Cation exchange capacity (CEC) was determined from Mehlich-3 analyses by sum of cations (Ross, 1995). Soil pH was determined in water (1:1, v/v) following the recommended method of Eckert and Sims (1995).

Soil samples for individual plot analyses were acquired at the time of first planting (2005) from the border of each plot to 10 cm depth with a 5 cm diameter Dutch auger, air-dried in a greenhouse at 40 °C, and sieved (2 mm). All soil and root samples acquired during the growing season were from the plot borders to avoid disruption of within-plot soil, which could affect erosion. Each sample was subject to phosphorus extraction with iron oxide-impregnated filter paper according to Chardon (2000). One gram of soil was agitated end-over-end at 4 rpm in 40 mL $CaCl_2$ in a tube with one strip of iron oxide-impregnated filter paper with a reactive surface area of 40 cm^2. The filter paper strips were then rinsed and dried, and phosphorus was desorbed for 1 h into 40 mL 0.1 M H_2SO_4, and the phosphorus concentration determined colorimetrically according to Murphy and Riley (1962). Samples from each plot were also analyzed for % organic matter by loss on ignition according to Nelson and Sommers (1996). Briefly, ~1 g soil was heated at 105 °C for 24 h, then cooled and weighed. Samples were then ignited in a muffle furnace at 400 °C for 16 h, then cooled and weighed, and % organic matter calculated by (weight$_{105}$ − weight$_{400}$)/weight$_{105}$.

2.4. Runoff measurements

Bulk runoff samples were collected from each hydrologically isolated plot after each runoff event, for a total of 11 events in 2005 (bean season) and 24 events in 2006 (bean, between seasons, and maize). Runoff volume was measured in each pre-calibrated collection bucket with a ruler. Each sample was then stirred and a subsample collected in a 400 mL plastic bottle. About 100 mL of each runoff sample was filtered (0.45 μm) following sample collection using a water aspirator pump. Filtered and unfiltered runoff samples were then acidified to pH 2 with 2–3 drops of concentrated HCl. Eighty mL of unfiltered runoff and 40 mL filtered runoff were then dried down into 20-mL glass vials at 60 °C in order to reduce shipment weight from Costa Rica to the USA. A preliminary study comparing 40 dried and undried runoff samples showed no difference in average total phosphorus concentrations ($p = 0.59$).

Runoff samples were re-suspended in 15 mL Millipore water and subjected to acid potassium persulfate digestion according to Pote and Daniel (2000). Sediment was mixed thoroughly into the solution, low pH values were verified by addition of phenolphthalein (50 mg mL^{-1} ethanol), and 0.5 g potassium persulfate was added to each sample. Sand-filled electric skillets were used as a heat source to digest multiple samples at one time for 2 h. After cooling, 2–3 drops of phenolphthalein solution was added to each sample and the pH raised with 10 M NaOH until a faint pink color was observed, and the sample was diluted with Millipore water to a volume of 100 mL. Digests of total phosphorus samples were then filtered, and phosphorus concentration of all digests was determined spectrophotometrically according to Murphy and Riley (1962). Particulate phosphorus was determined as the difference between total phosphorus and total dissolved phosphorus. Total solids content of runoff water was determined gravimetrically by weighing vials containing unfiltered dried runoff (sediment) and subtracting the weight of the cleaned empty vial after digestion. Since data sheets were lost for runoff volume of five runoff events during the maize 2006 season, rainfall, rainfall intensity, and previous runoff volumes were used to estimate missing values in order to calculate load values.

2.5. Statistical analyses

Data were analyzed using SPSS v. 11 (SPSS Inc., 2005). Data from each treatment were tested for normality and homogeneity of variance, and those not passing these tests were transformed (log or square-root) to achieve a normal distribution. The initial general linear model (GLM) to test for genotypic differences included year, site, genotype, fertilizer (high-P or low-P), and their interactions, as independent factors. Models were subsequently simplified to obtain the most parsimonious equation. If no transformation could adequately minimize differences in variance among treatments, Welch and Brown-Forsythe tests were used to confirm significance levels reported by the ANOVA model. Tukey's test was used for post-hoc analysis with all ANOVAs.

3. Results

3.1. Runoff measurements

3.1.1. Hydrology
Rainfall totaled 619 mm in the bean season of 2005, 620 mm in the bean season of 2006, 261 mm between seasons in 2006 and 526 mm during the maize season in 2006. Maximum intensity during a 1-h period reached 75 mm h^{-1} in the bean season of 2006, 36 mm h^{-1} between seasons in 2006 and 48 mm h^{-1} during the maize season in 2006. Rainfall during the bean season was similar to average rainfall for the area, but rainfall during the maize season in 2006 was uncharacteristically low due to el Niño weather patterns.

Table 2

Cumulative runoff and erosion over the 2005 and 2006 common bean growing seasons in Veracruz, Costa Rica. Values shown are average ± standard error. L-88 RILs were unreplicated at Site 1, as were Bribri and DOR363 low P treatments at Site 2.

	2005					2006				
	Total P (kg ha^{-1})	Dissolved P (kg ha^{-1})	Sediment (kg ha^{-1})	Runoff (mm)	Infilt. (% precip.)	Total P (kg ha^{-1})	Dissolved P (kg ha^{-1})	Sediment (kg ha^{-1})	Runoff (mm)	Infilt. (% precip.)
Site 1										
Bribri high P	0.66 ± 0.01	0.37 ± 0.09	1050 ± 226	17 ± 0.5	96 ± 0.3	0.24 ± 0.02	0.05 ± 0.01	784 ± 102	25 ± 3.7	93 ± 1.4
Bribri low P	0.40 ± 0.09	0.03 ± 0.00	1433 ± 253	22 ± 3.2	94 ± 1.0	0.17 ± 0.03	0.04 ± 0.00	1002 ± 179	31 ± 0.8	91 ± 0.3
DOR364 high P	0.50 ± 0.00	0.27 ± 0.06	976 ± 33.2	16 ± 0.2	96 ± 0.1	0.24 ± 0.05	0.05 ± 0.02	1272 ± 722	26 ± 4.2	93 ± 1.7
DOR364 low P	0.36 ± 0.07	0.04 ± 0.01	1383 ± 201	25 ± 3.6	93 ± 1.3	0.20 ± 0.02	0.02	1028 ± 206	30 ± 0.8	91 ± 0.25
L-88 14	0.52	0.04	2367	24	94	0.47	0.03	1404	29	92
L-88 30	0.26	0.03	788	19	95	0.16	0.05	541	27	93
L-88 43	0.47	0.02	1557	28	92	0.15	0.05	900	29	92
L-88 57	0.38	0.02	1293	29	92	0.21	0.04	1587	32	91
L-88 63	0.63	0.01	2113	27	93	0.2	0.02	752	28	92
L-88 67	0.52	0.03	1485	24	94	0.14	0.02	986	30	92
Site 2										
Bribri high P	0.08 ± 0.07	0.05 ± 0.05	53.3 ± 28.6	4.8 ± 0.2	99 ± 0.2	0.10 ± 0.04	0.03 ± 0.00	278 ± 69.0	7.4 ± 1.2	99 ± 0.2
Bribri low P	0.01	0.02	42.1	6.1	98	0.19	0.01	328	15	99
DOR364 high P	0.09 ± 0.05	0.11 ± 0.04	59.1 ± 6.68	6.1 ± 0.1	98 ± 0.5	0.05 ± 0.02	0.02 ± 0.00	182 ± 89.2	5.2 ± 0.3	99 ± 0.0
DOR364 low P	0.26	0.14	135.5	10.3	97	0.11	0.02 ± 0.00	216	11	98
L-88 14	0.04 ± 0.01	0.02 ± 0.01	74.4 ± 37.9	6.2 ± 1.4	98 ± 0.5	0.05 ± 0.01	0.01 ± 0.00	169 ± 49.6	6.5 ± 1.4	99 ± 0.4
L-88 30	0.02 ± 0.01	0.03 ± 0.01	40.4 ± 0.92	6.9 ± 1.3	98 ± 0.2	0.05 ± 0.01	0.01 ± 0.00	192 ± 82.1	6.9 ± 0.5	99 ± 0.2
L-88 43	0.05 ± 0.02	0.02 ± 0.00	134 ± 56.4	8.6 ± 3.0	97 ± 1.4	0.08 ± 0.01	0.01 ± 0.00	363 ± 80.0	10 ± 2.9	98 ± 0.8
L-88 57	0.01 ± 0.01	0.01 ± 0.00	26.6 ± 10.1	3.9 ± 0.5	99 ± 0.2	0.06 ± 0.04	0.01 ± 0.00	318 ± 63.1	8.2 ± 1.8	98 ± 0.6
L-88 63	0.04 ± 0.02	0.02 ± 0.00	83.6 ± 29.8	6.6 ± 1.1	99 ± 0.1	0.07 ± 0.04	0.01 ± 0.00	284 ± 128	8.0 ± 1.6	99 ± 0.3
L-88 67	0.03 ± 0.02	0.01 ± 0.00	76.3 ± 63.0	4.3 ± 2.0	99 ± 0.5	0.05 ± 0.01	0.02 ± 0.01	204 ± 12.4	6.6 ± 0.5	99 ± 0.1

Rainfall during common bean growing seasons averaged 43 mm per runoff event in 2005 and 41 mm per event in 2006. In both common bean seasons, the major rainfall events occurred within the first 30 days after planting (i.e., before the canopy achieved its maximum extent), with three events over 80 mm in 2005 and two events over 100 mm in 2006. These major events combined accounted for 83% of total sediment load in 2005 and 64% of total sediment load in 2006. Greater levels of runoff and erosion (10–$100\times$), and lower levels of rainfall infiltration (5%) were observed at Site 1 compared to Site 2 ($p < 0.001$; Table 2). Runoff volumes reached maximum collector capacity (indicating runoff overflow) at Site 1 in all plots after three rainfall events in 2005, five events in the common bean season, and three events in the maize season in 2006. At Site 2 runoff overflow occurred after one rainfall event at Site 2 in 2006. As such, the estimated contribution of these events to phosphorus and sediment loss under-represents their relative contribution to total losses over the study period.

3.1.2. Phosphorus

Particulate phosphorus concentration was correlated with sediment concentration in runoff ($p < 0.001$; Fig. 2). Greater dissolved phosphorus loads, but not total phosphorus loads, were observed in fertilized plots compared to unfertilized plots ($p = 0.009$). Total dissolved phosphorus loads over the common bean growing season were greater when fertilizer was applied, averaging 0.028–0.032 kg ha^{-1} at Site 1 and 0.023–0.013 kg ha^{-1} at Site 2 in unfertilized plots, and 0.318–0.053 kg ha^{-1} at Site 1 and 0.082–0.027 kg ha^{-1} at Site 2 in fertilized plots (2005–2006). Phosphorus enrichment ratios (mg total phosphorus kg^{-1} sediment/mg total phosphorus kg^{-1} soil) were 0.87 ± 0.08 to 1.03 ± 0.14 at Site 1 and 2.49 ± 0.39 to 4.81 ± 0.96 at Site 2 (2005–2006).

3.1.3. Plant and runoff/erosion interactions

Phosphorus loss through biomass removal greatly exceeded (>10 times) phosphorus lost through erosion in all treatments in both common bean and maize (Table 3). In 2006, when ground-cover by plants and organic matter was measured every 2 weeks, sediment concentration ($p < 0.001$) and sediment load ($p < 0.001$) were correlated in a multiple regression to groundcover, rainfall, rainfall intensity, and days after planting. Direct relations between groundcover and eroded sediment concentration were observed before maximum plant cover in 2005 and 2006 (Fig. 3). Genotype/phosphorus treatment, site, and year affected cumulative eroded sediment load ($p < 0.001$), total phosphorus load ($p < 0.001$), and runoff ($p < 0.001$) over both common bean seasons. Post-hoc Tukey's tests revealed genotypic effects in runoff and erosion over both years, with L-88 30 consistently in letter groups with least runoff and erosion, and DOR364 low-P and Bribri low-P
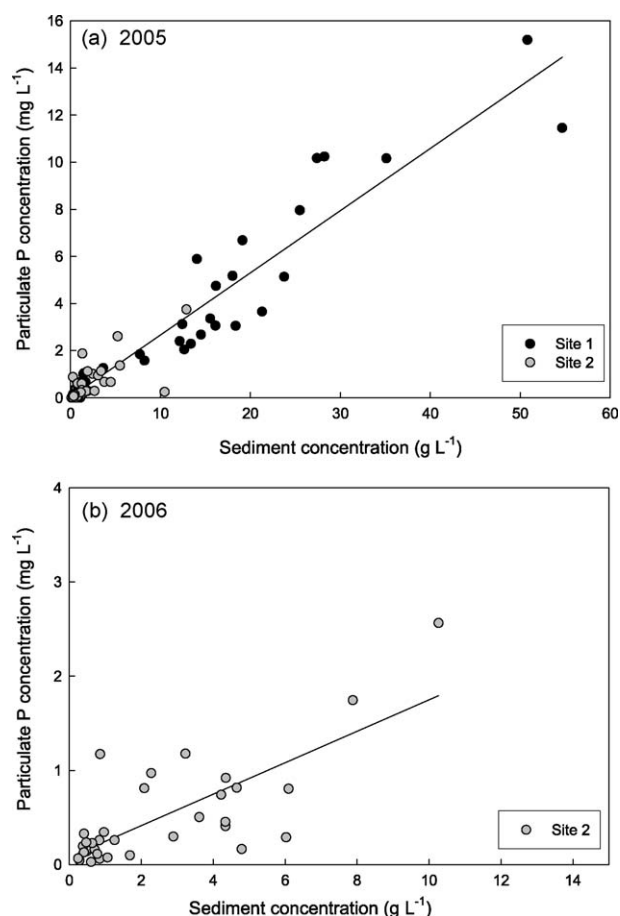

Fig. 2. Particulate phosphorus concentration (mg L^{-1}) was correlated with sediment concentration (g L^{-1}) in runoff in (a) 2005 ($r^2 = 0.91$, $p < 0.001$, $y = 0.0288 + 0.264x$) and (b) 2006 ($r^2 = 0.584$, $p < 0.001$, $y = 0.0776 + 0.167x$), indicating that erosion was the major cause of phosphorus loss due to rainfall. Results shown are from major rainfall events in unfertilized plots at both sites in 2005 and from Site 2 in 2006.

consistently in the homogeneous subset having the greatest runoff and erosion.

In order to factor out hydrologic effects on genotype performance, concentrations of phosphorus and sediment were analyzed in a time series over both common bean seasons (Fig. 4). On average, total phosphorus and sediment concentrations decreased with time ($p < 0.05$). Total phosphorus and sediment concentrations were consistently lowest in genotype L-88 30 over both years.

Table 3
Phosphorus budget from unfertilized plots at two sites in Veracruz, Costa Rica, in 2006 when plant P and eroded P were continuously monitored from planting of the common bean crop (May 23) through harvest of the maize crop (November 16). Values shown are average ± standard error.

|	Common bean (kg ha^{-1})	Between seasons (kg ha^{-1})	Maize (kg ha^{-1})	Crop cycle total (kg ha^{-1})
Site 1				
Eroded sediment	1021 ± 95.6	385 ± 46.7	60.8 ± 21.8	1468 ± 131
Eroded P	0.20 ± 0.03	0.23 ± 0.02	0.05 ± 0.01	0.53 ± 0.04
P in harvested grain	1.68 ± 0.26		2.73 ± 0.19	4.51 ± 0.37
P in residue after harvest	0.84 ± 0.40		3.24 ± 0.25	4.08 ± 0.78
Site 2				
Eroded sediment	257 ± 30.7	48.6 ± 14.2	35.3 ± 13.1	341 ± 37.0
Eroded P	0.07 ± 0.01	0.05 ± 0.01	0.04 ± 0.01	0.15 ± 0.02
P in harvested grain	1.94 ± 0.17		0.49 ± 0.03	2.45 ± 0.22
P in residue after harvest	0.53 ± 0.07		3.18 ± 0.28	3.76 ± 0.35
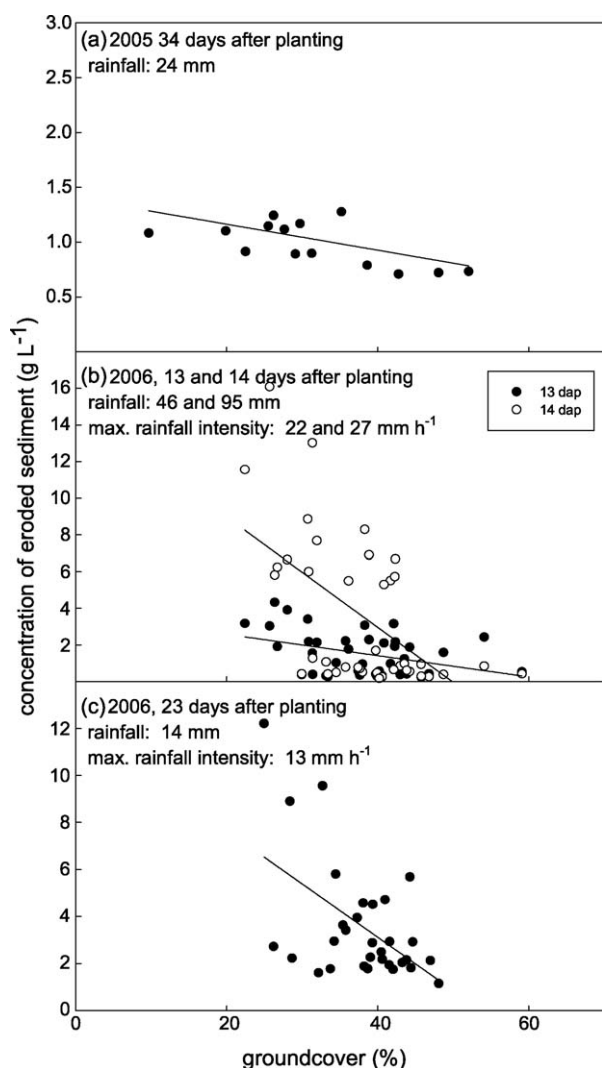
Fig. 3. Sediment erosion decreased with groundcover in (a) 2005 at 34 dap ($r^2 = 0.406$, $p = 0.014$); (b) 2006 at 13 days after planting ($r^2 = 0.154$, $p = 0.012$); and 14 dap at Site 1 ($r^2 = 0.258$, $p = 0.045$); and (c) 2006 at 23 days after planting ($r^2 = 0.275$, $p = 0.002$).

3.2. Plant measurements

3.2.1. Yield

Application of additional phosphorus increased yield ($p < 0.001$). Plot yield estimated from five plants sampled at harvest (yield$_{est}$) correlated well with yield collected from the whole plot (yield$_{meas}$) in 2005 (yield$_{est}$ = 260 + 1.314 × yield$_{meas}$; $r^2 = 0.646$) and 2006 (yield$_{est}$ = 103.8 + 0.548 × yield$_{meas}$; $r^2 = 0.761$). Lower yields in 2006 were due to the occurrence of a strain of cowpea chlorotic mottle virus that reduces seed set but does not affect other attributes of plant growth. Phosphorus harvest index (kg P in harvested grain kg^{-1} P uptake in shoots) varied among genotypes ($p < 0.001$), with L-88 30 having the lowest and Bribri high-P having the greatest phosphorus harvest index (Table 4). Phosphorus harvest index in maize averaged 0.46 ± 0.04 kg kg^{-1} at Site 1 and 0.15 ± 0.02 kg kg^{-1} at Site 2. Maize yields at Site 2 were low due to delayed planting.

3.2.2. Shoots

Biomass sampled pre-harvest did not differ among treatments, but biomass at harvest differed among treatments in 2006 ($p = 0.023$), with L-88 63 having the smallest average biomass

and DOR364 high-P the greatest. Plant density at harvest (2005–2006) averaged 13.0 ± 1.0 to 8.50 ± 0.58 plant m^{-2} at Site 1 and 10.9 ± 0.64 to 7.33 ± 0.42 plant m^{-2} at Site 2, and was similar among genotypes. In all treatments (2005–2006), the majority of phosphorus in bean biomass at harvest was in the grain (1.9–4.0 kg ha^{-1} in low-phosphorus soil and 3.1–7.3 kg ha^{-1} in fertilized soil), and phosphorus remaining in the crop residue averaged 0.52–1.29 kg ha^{-1} in low-phosphorus soil and 0.54–1.67 kg ha^{-1} in fertilized soil (Fig. 5). Maize phosphorus uptake averaged 4.48 ± 0.4 kg ha^{-1}, with major pools in the harvested grain (25.6 ± 3.8% of biomass phosphorus) and also in the residue leaf tissue (23.8 ± 1.3% of biomass phosphorus).

In 2005 plant groundcover, measured as percent of the overhead view, varied among genotypes 34 days after planting ($p = 0.013$), with L-88 43 and DOR364 low-P having the least groundcover and L-88 14 and L-88 67 having the most (Table 5), but values were similar at 71 days after planting. In 2006, plant groundcover was measured more frequently and varied among genotypes at 28 ($p < 0.001$) and 42 ($p < 0.001$) days after planting, with L-88 57 and L-88 67 having the least groundcover and L-88 30 and the high-P commercial genotypes having the most. Maximum plant groundcover was measured at 56 days after planting in 2006 and ranged from 37% in Bribri low-P to 66% in DOR364 high-P among the commercial genotype treatments, and from 49% in L-88 14 to 59% in L-88 30 among RILs under low phosphorus. Similarly, total visible groundcover (plants and organic matter) varied among genotypes at 28 and 42 days after planting ($p < 0.001$; Fig. 6). No difference in total visible groundcover was observed among genotypes at planting, but Site 1 had 27% less organic matter cover than Site 2 ($p < 0.001$). No differences in groundcover were observed between fertility treatments in 2005, but in 2006, the fertilized plots had a greater groundcover than did the low-phosphorus plots at 28 ($p < 0.001$), 42 ($p < 0.001$), and 56 ($p < 0.023$) days after planting.

3.2.3. Roots

Root length densities were generally low, with mostly fine roots appearing in the soil cores acquired mid-way between plants. Root length density of bean averaged 2.15 cm cm^{-3} at the 0–15 cm soil depth, 0.73 cm cm^{-3} at 15–30 cm, and 0.41 cm cm^{-3} at 30–45 cm (Table 5). Specific root length of common bean averaged 0.97 m g^{-1} at the 0–15 cm soil depth, 1.3 m g^{-1} at 15–30 cm, and 1.6 m g^{-1} at 30–45 cm.

Root growth in both bean seasons varied among genotypes at the 30–45 cm soil depth, specifically in root length density ($p = 0.045$), percent of total root mass in the soil core ($p = 0.041$), and specific root length ($p = 0.002$). Recombinant inbred lines L-88 43, L-88 30, and L-88 63 showed the most root growth at the 30–45 cm depth. Specific root length decreased with yield in the 0–15 cm soil depth in 2005 ($r^2 = 0.253$, $p = 0.024$) and with plant groundcover in the 30–45 cm depth in 2006 ($r^2 = 0.276$, $p = 0.002$). In 2006, more soil core replicates were acquired, and plant groundcover on day 42 increased with total root length in the soil core ($r^2 = 0.177$, $p = 0.013$), total root mass in the soil core ($r^2 = 0.377$, $p < 0.001$), and root length density in the top 15 cm of soil ($r^2 = 0.202$, $p = 0.008$; Fig. 7). Harvested biomass was independent of root shallowness.

4. Discussion

Contrary to expectations, phosphorus removed in seed yield exceeded phosphorus lost through erosion. Losses of phosphorus via erosion were less than expected probably because of low soil phosphorus content and high infiltration rates. Our results support the hypothesis that genotypes with shallow roots will acquire more phosphorus from the soil, resulting in greater ground cover and thereby less phosphorus loss in erosion. These results indicate
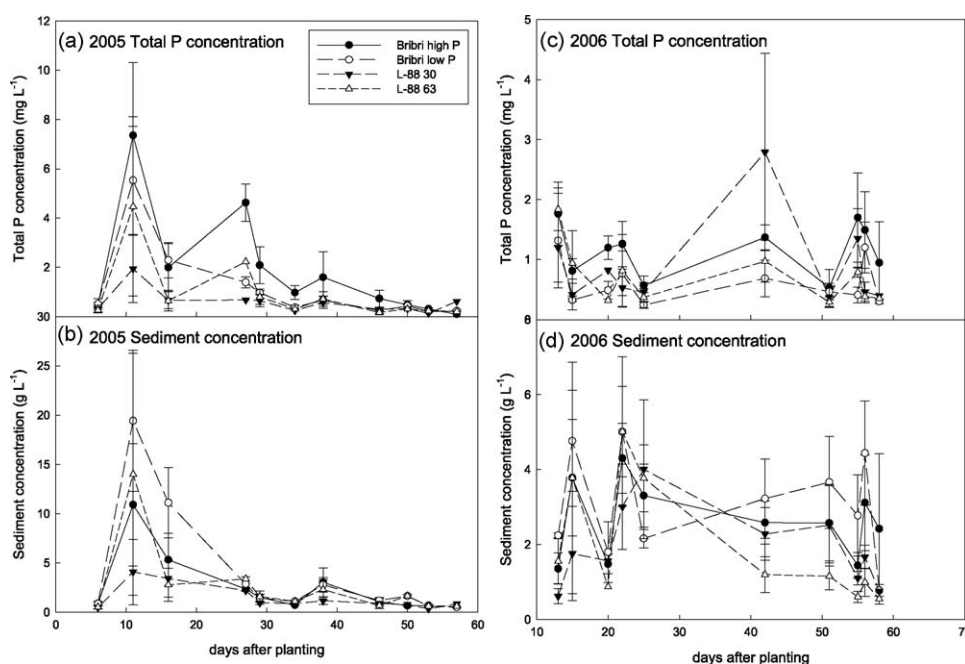
Fig. 4. Total phosphorus and sediment concentrations in runoff in (a and b) 2005 and (c and d) 2006. For clarity, only one of the commercial genotypes (Bribri: high and low P treatments) and RILs L-88 30 (shallow-rooted) and L-88 63 (deep-rooted) are shown.

that in low-input systems, breeding for nutrient-extractive crop genotypes must be balanced with other components of integrated nutrient management to avoid nutrient mining.

Phosphorus removal through biomass at harvest greatly exceeded phosphorus removal by erosion despite high rainfall intensities and steep slopes (Table 3). While plant phosphorus uptake and removal at harvest were of expected magnitudes (Fig. 5), phosphorus removal in runoff was low (Table 2). Low soil phosphorus levels at the study sites as well as unexpectedly high rainfall infiltration (resulting in low runoff volumes) may account for the low-phosphorus erosion rates. Phosphorus harvest index values obtained here (Table 4) were slightly lower than those measured on other common bean genotypes by Araújo and

Teixeira (2003). Putthacharoen et al. (1998) reported greater phosphorus removal in harvested products of maize (44 kg phosphorus ha^{-1}) and mung bean (15 kg phosphorus ha^{-1}) 1) from a Quartzipsamment field in Thailand compared to those in the present study, but their soil had greater phosphorus availability (21 kg Bray II phosphorus ha^{-1}). As in the present study, the authors also reported that removal of nutrients by crop harvest exceeded those lost through erosion, although only extractable nutrient levels were measured. These results illustrate the importance of empirical studies for understanding nutrient balances, since site characteristics widely vary among agro-ecosystems and are difficult to describe with universal models.

Table 4

Biomass, yield, and phosphorus harvest index in common bean genotypes differing in root architecture. Values shown are the average of both sites ± standard error. Letters indicate significantly different subsets among genotypes as determined by a Tukey's test on data from each year separately. Biomass was not significantly different among genotypes in 2005 ($p = 0.147$).

	Biomass (kg ha^{-1})	Grain yield (kg ha^{-1})	PHI[a] (kg grain P kg^{-1} shoot P)
2005			
Bribri high P	4837 ± 916	3078 ± 576b	0.86 ± 0.00c
Bribri low P	3042 ± 451	1838 ± 239ab	0.86 ± 0.02c
DOR364 high P	4689 ± 1757	2586 ± 919ab	0.80 ± 0.04bc
DOR364 low P	2406 ± 602	1194 ± 267ab	0.77 ± 0.03abc
L-88 14	3282 ± 792	1584 ± 432ab	0.76 ± 0.02abc
L-88 30	4054 ± 311	1755 ± 114ab	0.69 ± 0.07ab
L-88 43	2359 ± 743	947 ± 287a	0.66 ± 0.01a
L-88 57	2904 ± 566	1344 ± 222ab	0.65 ± 0.04a
L-88 63	2424 ± 539	1138 ± 211ab	0.76 ± 0.03abc
L-88 67	3655 ± 571	1968 ± 400ab	0.82 ± 0.04bc
2006			
Bribri high P	1511 ± 203ab	1000 ± 149bc	0.88 ± 0.01c
Bribri low P	983 ± 223ab	629 ± 176abc	0.84 ± 0.03bc
DOR364 high P	1900 ± 358b	1058 ± 160c	0.84 ± 0.03bc
DOR364 low P	1224 ± 197ab	773 ± 142abc	0.87 ± 0.01bc
L-88 14	1165 ± 209ab	641 ± 104abc	0.80 ± 0.02bc
L-88 30	1275 ± 243ab	557 ± 138abc	0.64 ± 0.01a
L-88 43	1170 ± 210ab	598 ± 127abc	0.76 ± 0.02b
L-88 57	802 ± 156a	379 ± 64.0ab	0.77 ± 0.04bc
L-88 63	1377 ± 188ab	797 ± 108abc	0.84 ± 0.01bc
L-88 67	657 ± 77.8a	353 ± 54.0a	0.85 ± 0.02bc

[a] PHI = phosphorus harvest index (kg grain P kg^{-1} shoot P).
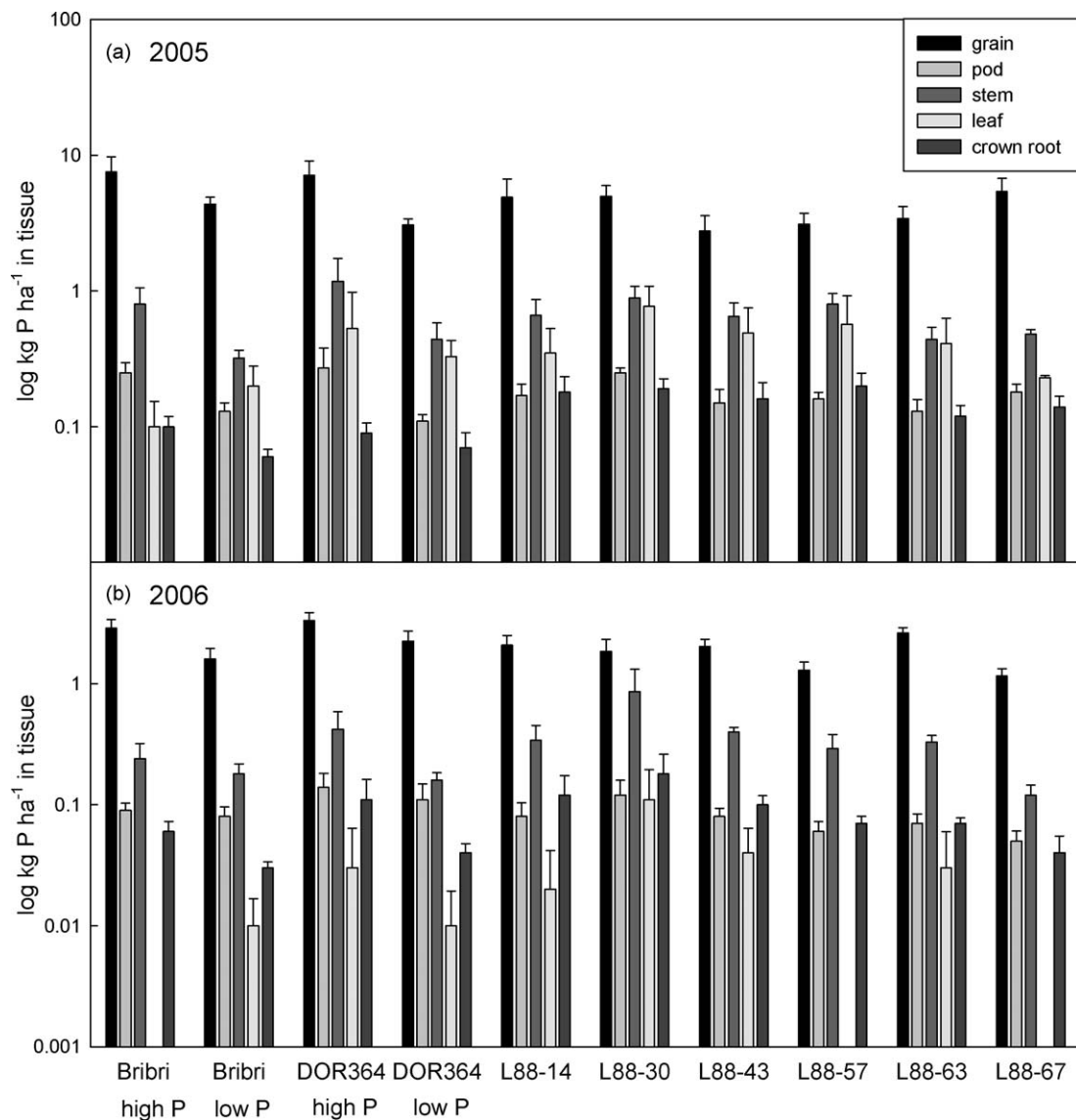
Fig. 5. (a and b) Phosphorus partitioning in plant tissue at harvest in common bean genotypes differing in root architecture, on a log scale. Values shown are the average of both sites ± standard error. The sum of the bars represents total phosphorus in biomass for each genotype.

In this study, genetic effects on soil phosphorus depletion by erosion were observed and could largely be explained by variability in root shallowness. From 2005 to 2006, we observed a 20–50% variation in groundcover among L-88 RILs under low phosphorus, which in turn led to a 50–80% reduction in sediment loss. The dynamics between root architecture and erosion were linked by the relationships of these components with groundcover, as in the following example of two genotypes (L-88 30 and L-88 63) contrasting in root architecture, groundcover, and subsequently erosion. Genotype L-88 30 had a higher percentage of shallow roots (roots in the 0–15 cm soil depth compared to total root length in the soil core; Table 5), with typical yields but greater biomass and phosphorus uptake (Table 4 and Fig. 5), and had consistently lower total phosphorus and sediment concentrations in runoff compared to the RILs that had lower percentages of shallow roots (Fig. 4). Conversely, L-88 63 showed a higher percentage of deep roots (Table 5), less groundcover (Fig. 6), and consequently increased total phosphorus and sediment loads compared to other L-88 RILs (Table 2). These trends suggest a connection between root shallowness and erosion through improved plant groundcover (Figs. 3 and 7), indicating that selection for root shallowness can both improve plant performance and reduce erosion.

The genetic variation in root shallowness and shoot growth among L-88 RILs that decreased erosion is important for the sustainability of this agro-ecosystem since considerable sediment loss was observed in this study. In addition to nutrient depletion, erosion represents a significant cost to producers since loss of topsoil leads to decreased yields through the loss of a suitable root growth environment. For example, artificial soil removal studies have shown that yield is reduced by increasing amounts when increasing depths of soil are removed, and in some cases no fertilizer combinations can restore productivity (Lal, 1995). Eroded sediment contains much higher nutrient concentrations than the bulk soil due to the preferential erosion of fine particles that tend to have greater surface area and sorption capacity (Sharpley, 1985), as illustrated by the phosphorus enrichment ratios that range up to 4.81 measured in this study. Furthermore, loss of topsoil represents an important nutrient loss to the system since phosphorus in the topsoil is more available to the plant than the recalcitrant phosphorus in the subsoil (Nye and Foster, 1961).

Application of phosphorus fertilizers can be viewed as an amendment to highly sorbed phosphorus by saturating sorption sites on soils, but fertilizer levels required to achieve this may present prohibitive costs to the producer. Organic inputs through

Table 5
Root length density with depth and measured crop canopy cover (day 34 in 2005 and day 28 in 2006) from common bean growing seasons in Veracruz, Costa Rica. Values shown are average ± standard error. In 2005, root samples were only acquired from RIL plots. Letters indicate significantly different subsets among genotypes as determined by a Tukey's test on data from each year separately.

	Root length density (cm cm^{-3})			Crop canopy cover (%)
	0–15 cm	15–30 cm	30–45 cm	
2005				
Bribri high P				17.75 ± 4.21a
Bribri low P				28.37 ± 2.53ab
DOR364 high P				25.26 ± 3.46ab
DOR364 low P				37.92 ± 5.80ab
L-88 14	2.43 ± 0.29	0.55 ± 0.22	0.19 ± 0.06	38.15 ± 6.32ab
L-88 30	2.02 ± 0.27	0.52 ± 0.10	0.74 ± 0.32	25.52 ± 2.61ab
L-88 43	1.54 ± 0.39	0.74 ± 0.21	0.58 ± 0.26	21.40 ± 2.26ab
L-88 57	1.82 ± 0.35	0.64 ± 0.40	0.29 ± 0.15	35.86 ± 9.35ab
L-88 63	1.31 ± 0.37	0.52 ± 0.22	0.45 ± 0.18	24.50 ± 6.00ab
L-88 67	1.00 ± 0.29	0.52 ± 0.45	0.18 ± 0.15	44.24 ± 2.74b
2006				
Bribri high P	2.26 ± 0.71ab	0.48 ± 0.19	0.36 ± 0.23	20.51 ± 1.81ab
Bribri low P	2.14 ± 0.05ab	0.49 ± 0.12	0.33 ± 0.31	15.65 ± 3.26a
DOR364 high P	2.92 ± 0.32ab	1.24 ± 0.24	0.31 ± 0.14	29.37 ± 3.89bc
DOR364 low P	3.91 ± 0.45b	1.19 ± 0.48	0.23 ± 0.04	38.80 ± 1.54c
L-88 14	2.89 ± 0.99ab	1.02 ± 0.28	0.34 ± 0.16	17.01 ± 2.85a
L-88 30	2.33 ± 0.29ab	0.86 ± 0.31	0.56 ± 0.23	19.26 ± 1.81ab
L-88 43	2.67 ± 0.84ab	1.01 ± 0.39	0.89 ± 0.20	18.12 ± 2.76ab
L-88 57	1.29 ± 0.19a	0.42 ± 0.13	0.18 ± 0.07	14.39 ± 2.83a
L-88 63	1.96 ± 0.36a	0.69 ± 0.09	0.48 ± 0.10	13.68 ± 2.50a
L-88 67	2.34 ± 1.29a	0.68 ± 0.09	0.19 ± 0.09	14.71 ± 2.57a

crop residue are more readily employed, and in combination with certain management practices may be more practical (Kaizzi et al., 2007). Drinkwater and Snapp (2007) emphasized the value of organic sources of plant nutrients as an ecological approach to nutrient management and increasing nutrient mean residence time. It should be noted that considerable phosphorus levels remained in the crop residue after harvest in this study (Fig. 5), illustrating the importance of management practices such as retaining residue for increasing sustainability in this agro-ecosystem.

The growth of unfertilized RILs with shallow root architecture was comparable to that of fertilized commercial genotypes. The advantage of shallow L-88 lines over improved commercial genotypes illustrates the importance of root traits for plant growth in low-phosphorus soils. Unfertilized L-88 RILs showed similar total phosphorus accumulation, harvested biomass, phosphorus harvest index, and groundcover (Table 4, Figs. 5 and 6) compared to the fertilized commercial genotypes. Although commercial genotypes DOR364 and Bribri are commonly grown and had the greatest yield, this was due to improved phosphorus harvest index compared to the L-88 RILs. Percent groundcover in the unfertilized commercial genotypes was lower compared to the L-88 RILs (Fig. 6), and consequently, the commercial genotypes in unfertilized plots consistently showed greater runoff than L-88 RILs in unfertilized plots. Since the L-88 RILs were selected for root traits and had not yet been bred for yield in this environment, these results suggest that breeding for both phosphorus harvest index and root shallowness could result in higher yielding lines that also have improved groundcover to reduce erosion.

Application of phosphorus fertilizer also improved soil conservation by reducing sediment loss. In both years, the majority of phosphorus and sediment erosion occurred before maximum
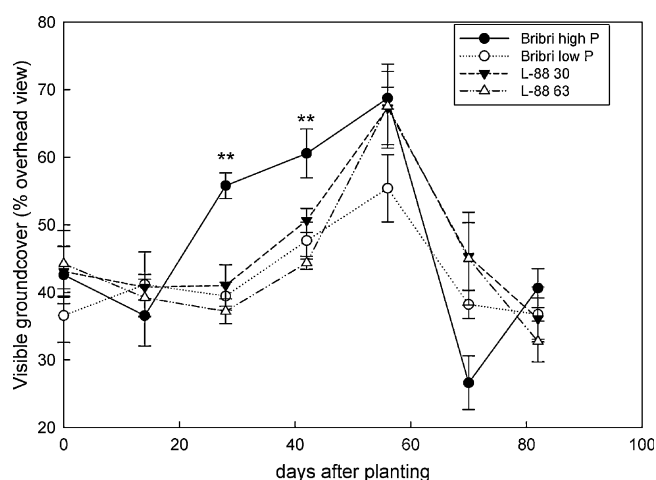

Fig. 6. Changes in percent groundcover (plants and organic matter) throughout the 2006 common bean growing season. For clarity, only one of the commercial genotypes (Bribri: high and low P treatments) and RILs L-88 30 (shallow-rooted) and L-88 63 (deep-rooted) are shown. **Significant differences among genotypes ($p < 0.001$).
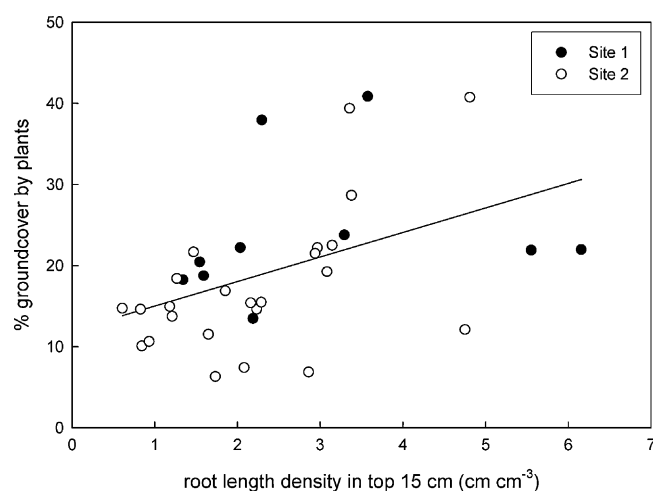

Fig. 7. Percent groundcover by plants 42 days after planting increased with root length density in the upper 15 cm of soil ($r^2 = 0.2$, $p = 0.008$) in the 2006 common bean season. Data from Sites 1 and 2 were pooled since values were similar for both groundcover ($p = 0.181$) and root length density ($p = 0.160$).

canopy closure was reached (i.e., within 30 DAP), which is related to both reduced groundcover and also the timing of major rainfall events. Therefore early canopy cover is essential for reducing erosion, particularly given the rainfall patterns in this agro-ecosystem in the central highlands of Costa Rica. The fertilized plots showed notably early groundcover compared to unfertilized plots (Fig. 6), indicating an advantage of increasing available phosphorus levels through fertilizer application that was not seen with variability in root shallowness.

Plant resource allocation is another important factor that affected erosion and phosphorus cycling in this agro-ecosystem. RILs L-88 43, L-88 63, and L-88 30 were the deepest rooted genotypes, as measured by root length density at 30–45 cm (Table 5). In the case of L-88 30, this can be explained by an allometric effect since L-88 30 also had a greater shoot biomass (Table 4), reflected by improved growth overall. Interestingly, L-88 30 also showed the lowest phosphorus harvest index, indicating resource allocation to tissue other than the grain, which affected runoff and erosion (discussed below). It appears possible for breeders to select for both root distribution with depth and resource allocation within the plant, as illustrated by the variation in these traits among L-88 RILs. Since these traits affect plant groundcover, which is largely responsible for crop-associated variability in runoff and erosion, these results suggest that breeding for soil conservation traits within a species is possible.

Scaling up from a subsample to whole-plot level can be difficult in this kind of agricultural system in which multiple seeds are planted together, resulting in variable plant sizes. In this study, healthy representative plants in a range of sizes were acquired for the subsamples. In 2006, plants most representative of typical yields (not virus-affected) were selected for the subsamples. The lower slope between subsample yield and whole-plot yield in 2006 was due to the incidence of cowpea chlorotic mottle virus. The correlations between yield scaled up from the subsample and yield measured from the whole plot show that this was an accurate method of subsampling for scaling up to the whole-plot level.

Variability in plant performance was observed between years and sites. The improved average plant performance and phosphorus uptake values in 2005 compared to 2006 were likely due to the greater fertilizer application in 2005. Due to planting pattern (a grid pattern with 2–3 seeds every 40 cm) and sub-optimal growth (likely from aluminum toxicity as well as nutrient deficiencies), plots never reached complete canopy closure as is often seen in common bean fields elsewhere sown in rows. Total visible groundcover at planting indicated that baseline organic matter cover did not differ among treatments, but was greater at Site 2 than Site 1. These attributes partly explain differences in runoff and erosion between sites, as discussed below.

The high degree of correlation between particulate phosphorus concentration and sediment concentration in runoff (Fig. 2) shows that erosion was the major cause of phosphorus loss due to rainfall. At Site 1, the lower slope of particulate phosphorus vs. sediment concentration during major rainfall events in 2006 and increased variability in runoff and erosion in general reflects in part the effects of runoff overflow from the collection containers. Although much higher than runoff and erosion values observed at Site 2, values presented here for Site 1 during common bean and maize seasons are likely an underestimate of phosphorus loss since problems with overflow likely reduced the amount of fine particles collected, which are more concentrated in phosphorus. Barton et al. (2004) reported erosion rates of 3.29 t ha^{-1} season^{-1} in a no-till Ultisol of Yunnan, China, planted with maize, which exceed the erosion rates of <1 t ha^{-1} season^{-1} observed in the present study. Many factors including rainfall intensity and timing, organic cover, and soil characteristics likely describe these differences in erosion rates. As in the present study, Barton et al. (2004) noted much lower erosion

rates than expected, illustrating the importance of empirical erosion studies, and implying that some erosion models and nutrient balance calculations may over-estimate rates of soil loss.

Variability among agro-ecosystems that results in wide ranges of erosion rates are exemplified by the differences in erosion between the two sites in this study. Although both sites were similar in slope, soil type, and plant performance, and were located within ∼2 km of each other, runoff and erosion values were much greater at Site 1. Plots at Site 2 had greater organic matter cover, which has been well characterized to increase infiltration and reduce erosion by absorbing water and protecting soil aggregates from destruction by raindrops (Mannering and Meyer, 1963). Furthermore, Site 1 had a history of more intensive land use with reduced groundcover, which led to a higher degree of soil degradation, deteriorated soil structure and reduced capacity for infiltration. Because of these differences in site characteristics, runoff and erosion data at Site 1 were analyzed separately from those at Site 2. Interestingly, similar rankings in erosion among L-88 RILs were observed at both sites, particularly in 2005 (Table 2). This shows that the advantages in reduced erosion conferred by variability in shoot growth among RILs was consistent over different environments.

Trends in runoff and erosion among fertility treatments were as expected, with fertilized plots showing increased phosphorus loss but decreased sediment loss due to increased plant groundcover (Table 2). Site characteristics and fertilizer application explain much of the variability in phosphorus erosion observed in this study. Lower average phosphorus enrichment ratios at Site 1 reflect lower clay contents in surface soil compared to Site 2. Increased dissolved phosphorus concentrations in runoff were also expected from fertilized plots and again reflect differences in land use since dissolved phosphorus increases in fertilized plots were greater at Site 1, due to lower sorption rates to soil solids at the site with lower surface clay levels. However, rapid sorption of fertilizer phosphorus to soil solids was observed in general, since 60 kg phosphorus ha^{-1} was applied, which greatly outweighs the sum of average total biomass phosphorus (6.32 kg ha^{-1}) and total eroded phosphorus (0.038 kg ha^{-1}). Application of fertilizer improved yield by 37–40% for Bribri and 27–54% for DOR364, but a low percentage of the applied fertilizer was used by the plant and some was lost to runoff and erosion. Meanwhile, variability in root traits resulted in improved shoot growth and yield in some genotypes without any external inputs, including in crop residues which could be used to fertilize subsequent crops. These results illustrate the importance of cost/benefit analyses for inputs and outputs in nutrient budgeting, for example cost of fertilizer vs. increased income due to fertilizer use, especially in complex low-input agro-ecosystems where resources are scarce.

5. Conclusions

In this study, genotypic differences in root architecture of common bean led to variation in groundcover by shoots, which in turn affected runoff and erosion. Thus, genetic variation for a root trait, in this case root shallowness, reduced erosion, suggesting that such genotypes can improve the sustainability of low-input agro-ecosystems. Although phosphorus-extractive genotypes reduced soil erosion, this benefit was outweighed by greater phosphorus loss in seed yield, since phosphorus removed through seed yield and plant biomass at harvest greatly exceeded phosphorus loss via erosion. Fertilized plots showed improved plant productivity, but only slightly reduced erosion. The majority of phosphorus applied in fertilizer was rapidly sorbed to soil solids. However, we measured substantial phosphorus levels remaining in crop residues after harvest that varied by genotype. Over the long term, residue management could provide a practical means of

improving phosphorus availability in surface soil, with up to 2.1 kg ha^{-1} residue P returned by common bean per year.

Few studies have been reported on the potential of crop breeding for reduced soil nutrient depletion. Our results indicate that selection for root traits such as shallowness in combination with integrated nutrient management is a promising strategy for improving both productivity and sustainability in sloped low-input tropical agro-ecosystems.

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